



Long-term monitoring reveals widespread and severe declines of understory birds in a protected Neotropical forest

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Long-term studies on the population dynamics of tropical resident birds are few, and it remains poorly understood how their populations have fared in recent decades. Here, we analyzed a 44-y population study of a Neotropical understory bird assemblage from a protected forest reserve in central Panama to determine if and how populations have changed from 1977 to 2020. Using the number of birds captured in mist nets as an index of local abundance, we estimated trends over time for a diverse suite of 57 resident species that comprised a broad range of ecological and behavioral traits. Estimated abundances of 40 (~70%) species declined over the sampling period, whereas only 2 increased. Furthermore, declines were severe: 35 of the 40 declining species exhibited large proportional losses in estimated abundance, amounting to $\geq 50\%$ of their initial estimated abundances. Declines were largely independent of ecology (i.e., body mass, foraging guild, or initial abundance) or phylogenetic affiliation. These widespread, severe declines are particularly alarming, given that they occurred in a relatively large (~22,000-ha) forested area in the absence of local fragmentation or recent land-use change. Our findings provide robust evidence of tropical bird declines in intact forests and bolster a large body of literature from temperate regions suggesting that bird populations may be declining at a global scale. Identifying the ecological mechanisms underlying these declines should be an urgent conservation priority.

tropical birds | population declines | intact forest | biodiversity loss | long-term studies

Anthropogenic stressors such as land-use change and climate change pose an existential threat to the integrity of tropical systems, which harbor a disproportionate amount of global biodiversity relative to other biomes (1–3). Deforestation in the humid tropics accelerated 62% between 1990 and 2010 (4), resulting in a net loss of ~ 8 million ha y^{-1} during this time period (5), and losses have continued to accrue in recent years (6). Increasing temperatures are driving upslope range shifts of lowland tropical species across taxa (7, 8), and both theoretical and empirical evidence indicate that tropical biotas are more strongly affected than their temperate counterparts (9–11). Changing rainfall regimes in the tropics are also expected to strongly impact species' distributions and population dynamics (3, 12). Given the global importance of tropical forests with respect to carbon storage and biological diversity, conserving tropical ecosystems and mitigating the impacts of anthropogenic change is an increasingly urgent research priority (1).

Long-term monitoring programs are the gold standard for characterizing temporal changes in populations and communities and assessing the impacts of anthropogenic change on biodiversity (13). For example, continent-wide monitoring programs such as the North American Breeding Bird Survey (reviewed in ref. 14) or the Pan-European Common Bird Monitoring Scheme (<https://pecbms.info/trends-and-indicators/species-trends/>) have revealed aggregate losses of billions of birds in recent decades (15–19). These declines span biomes and include both common and rare species of diverse ecologies and life histories (15, 17, 20–22), stimulating widespread concern over the conservation prospects of birds worldwide.

In contrast to species at temperate latitudes, comparatively little is known about long-term trends of resident tropical bird populations (23). Tropical bird communities are notoriously challenging to survey because they are hyperdiverse, with many rare and cryptic species that are difficult to detect or count accurately (23, 24). Nevertheless, a handful of studies have provided insight into how resident tropical bird populations have fared in recent decades and helped identify ecological traits underlying population trends. For example, certain guilds, such as understory or terrestrial insectivores, appear to be consistently declining in both intact (25, 26) and fragmented tropical forests (reviewed in ref. 27). Body size has also been implicated, with both small- (28) and large-bodied species (29) exhibiting declines or even extirpation following fragmentation. Finally, species that are rare or patchily distributed are more likely to decline or be extirpated following forest fragmentation (29, 30).

Significance

We leveraged a 44-y population study of Neotropical understory birds from a protected forest reserve in central Panama to document widespread and severe declines in bird abundance. Our findings provide evidence that tropical bird populations may be undergoing systematic declines, even in relatively intact forests. The implications of these findings are that biodiversity baselines may be shifting over time, and large tracts of tropical forest may not be sufficient for maintaining stable bird populations. Our study highlights the importance of long-term monitoring for detecting cryptic losses in biodiversity and motivates the need for future work drilling down to the underlying mechanisms to understand and mitigate future declines.

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The few long-term studies of bird populations from intact tropical forests have yielded mixed evidence. A 14-y study in a lowland rainforest bird community in Ecuador found decreases in both capture rates and visual observations of birds across forest strata and foraging guilds, with particularly steep declines in terrestrial insectivores (25). Although the mechanisms remain unclear, the study hypothesized that changes in the Southern Oscillation Index and increased rainfall in La Niña years at the study site played a role in the declines (25). Similarly, a 35-y study of rainforest bird populations at Manaus, Brazil, found steep declines among near-ground and terrestrial insectivores (26), which the study attributed to possible climate-driven changes in insect abundance. In contrast, an 18-y study of protected forests in Costa Rica found that communities were relatively stable over time (31). In general, so few studies have documented long-term avian population trends from intact forests that emergent patterns remain unclear.

Here, we leveraged a 44-y (1977 to 2020) population study of Neotropical understory birds—the longest study of its kind in the Neotropics—to evaluate long-term population trends from a large (~22,000-ha) protected forest reserve in central Panama. Using the number of unique individuals captured as an index of abundance, we modeled the populations of 57 resident bird species, with the goal of determining how their abundances had changed over the sampling period. Specifically, we estimated the annual and total proportional changes in abundance across the study period for each species. We also tested for associations between estimated trends and ecological traits that are commonly linked to variation in population dynamics (i.e., body mass, foraging guild, and local abundance). Based on the few studies published to date, we predicted steeper declines and greater proportional losses of abundance for species of smaller body size (28), terrestrial insectivores (25, 26), and species with low relative abundance (i.e., locally rare or patchy species; refs. 29 and 30).

Results

Overall, we found compelling evidence of widespread declines in abundances over the 44-y sampling period (1977 to 2020). Using the annualized proportional change (i.e., the rate of change over a single year) to estimate the direction of species' trends, we found that of the 57 resident species considered, 40 (~70%) declined in abundance, whereas only 2 species (a hummingbird [*Amazilia amabilis*] and a puffbird [*Malacoptila panamensis*]) increased (Fig. 1 and *SI Appendix, Figs. S5 and S6 and Table S2*). Abundances of 15 (26.3%) species did not change appreciably. Estimated trends varied substantially among the focal species (mean \pm SD = -0.03 ± 0.04), ranging from 0.06 (*A. amabilis*) to -0.15 (a flycatcher [*Mionectes olivaceus*]; *SI Appendix, Table S2*). Of the 19 bird families represented in our sample, all but one (Bucconidae) showed an aggregate decline in abundance (*SI Appendix, Fig. S7 and Table S2*). Declines were steepest among the order Passeriformes, with the highest rates of decline occurring in the families Vireonidae (vireos), Cardinalidae (cardinals), Oxyruncidae (sharpbill and allies), Tityridae (tityras), Furnariidae (ovenbirds), and Polioptilidae (gnatwrens; *SI Appendix, Fig. S7*).

Using the total proportional change (i.e., the total change in estimated abundance over the entire study) to estimate the magnitude of change in species' local abundances, we found that many of the declines were severe. Estimated losses ranged from 40 to 99.5% of species' initial abundances (mean \pm SD = 0.71 ± 0.18 ; *SI Appendix, Table S2*), and 35 of 40 (87.5%)

declining species lost more than 50% of their initial abundance (Fig. 2). A diverse group of nine species, from nine different bird families and including eight of nine foraging guilds, experienced total proportional losses of >90% across the study (*SI Appendix, Table S3*). These nine species, which include those that are more abundant in 1) younger and drier forests or 2) wetter foothill forests, are all likely extirpated from the study area or present only at very low densities.

We also estimated how the number of unique individuals captured on our two net lines in a given sampling period was expected to change over the course of the study (Δn). On average, we captured an estimated 1.64 ± 2.16 (mean \pm SD) fewer individuals per sampling period by the end of the study, with 10 species estimated to have ≥ 3 fewer individuals captured (*SI Appendix, Table S4*). The most commonly captured species, red-capped manakin (*Ceratotipra mentalis*), was estimated to show the greatest decline in the number of individuals captured on the two lines ($\Delta n = -13.79$; ~23 individuals per year in 1977 to ~9 individuals in 2020). Other species estimated to show heavy declines in the number of individuals captured included three ant-followers, three small-bodied understory insectivores, two terrestrial insectivores, and an understory hummingbird (*SI Appendix, Table S4*).

Species' ecological traits (body size, foraging guild, local abundance) did not account for interspecific variation in estimated trends (*SI Appendix, Table S5*). Annualized proportional change in abundance was not associated with foraging guild (Fig. 3), body mass (*SI Appendix, Fig. S8*), or initial local abundance (*SI Appendix, Fig. S9*). All foraging guilds exhibited negative trends, with arboreal omnivores declining at the steepest rates (Fig. 3). The guilds with the shallowest proportional declines were nectarivores and terrestrial frugivores. Contrary to our predictions, terrestrial insectivores did not decline more rapidly than other guilds (Fig. 3).

Discussion

We used the longest-running (44 y) demographic study of tropical forest birds (>80,000 net hours, >14,000 individuals captured) to reveal pervasive declines of understory species in a protected reserve in central Panama. From 1977 to 2020, 70% (40 of 57) of the understory bird species whose populations we modeled declined in abundance, irrespective of foraging guilds, taxonomic groups, body mass, or local abundance. In total, 35 of the 40 (87.5%) declines were severe, comprising $\geq 50\%$ losses relative to initial estimated abundances. The declines of rare species were concerning because they contribute disproportionately to community structure and ecosystem functioning (32–34). In addition, many of the most common species (e.g., red-capped manakin, the most abundant frugivore on the plot and an important seed disperser; ref. 35) suffered the greatest estimated losses in number of captures per sampling period on our net lines (i.e., 23 individuals captured per year in 1977, but 9 individuals captured per year in 2020), which has also likely resulted in a reduction of ecosystem services. We have no reason to believe that the areas sampled by this study are not representative of the larger region in which they are embedded or unique to this reserve.

The observed declines are alarming and represent some of the most drastic losses of bird populations documented in intact Neotropical forests. Results from other long-term studies in relatively intact forests have yielded mixed results with respect to temporal changes in bird populations. Similar to our findings, a 14-y study from lowland rainforest at Tiputini Biodiversity Station in

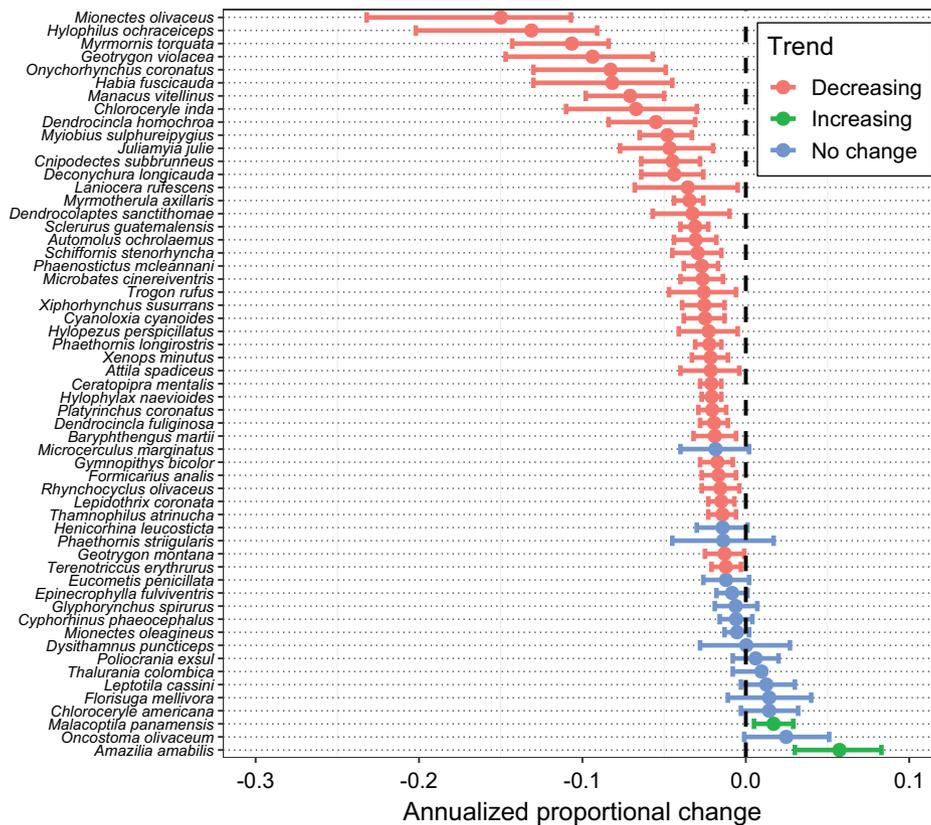


Fig. 1. Trends in estimated abundance of the 57 resident bird species across the 44-y sampling period (1977 to 2020) at the Limbo plot, Parque Nacional Soberanía, Panama. For each species, the mean estimate of annualized proportional change and 95% BCIs are shown. Trends were considered significant if the 95% CI did not cross zero (indicated by the vertical dashed line). Green = increase in abundance; blue = no change; red = decrease in abundance. Focal species are ranked in order of trend, from greatest decreasing trend (*Mionectes olivaceus*) to greatest increasing trend (*Amazilia amabilis*).

Ecuador found widespread avian declines (>80% of 28 species; ref. 25) spanning diverse foraging guilds, although terrestrial insectivores were disproportionately affected. Conversely, a 35-y study from primary lowland rainforest in Manaus, Brazil, showed that 11% (9 of 79) of species declined, most of which were terrestrial and near-ground insectivores, but the majority of other species and guilds did not (26). Finally, an 18-y study from Costa Rica (31) found no significant long-term changes in bird populations in protected forests.

In general, our findings represent the starkest evidence to date of avian community change in relatively large protected areas, which are often assumed to be reservoirs of biodiversity (36, 37). Interestingly, a recent study of demographic responses to seasonal drought among forest birds at our study site (38) used mark-recapture models to show that adult survival for most species remained stable and largely unchanged over 33 y (1978 to 2011), which could be viewed as contradicting the observed declines documented here. However, many species exhibited marked declines in recruitment and population growth rates in drier years (38), results which are broadly consistent with our findings and which suggest that reduced reproduction or increased offspring mortality could be responsible for the observed declines in local densities, rather than increased mortality of territorial breeding adults.

The pervasiveness of the long-term declines in Panama across diverse avian taxa suggests that multiple ecosystem-level processes may be interacting to generate this pattern. We had initially hypothesized that species that were small-bodied, terrestrial insectivores and, at low initial abundances, would exhibit the greatest declines, given findings from other studies (25, 26). We found equivocal evidence, however, that these

traits were associated with estimated rates of decline. For example, four of the eight terrestrial insectivores in our sample (song wren [*Cyborhinus phaecephalus*], white-breasted wood-wren [*Henicorhina leucosticta*], scaly-breasted wren [*Microcerculus marginatus*], chestnut-backed antbird [*Poliocrania exsul*]) did not change in abundance over the 44-y study. Similarly, species of all body sizes, foraging guilds, and initial abundances exhibited declines. Thus, the mechanisms underlying variation in species' trends over time remain unclear. Below, we outline possible processes that may be underlying the declines and suggest future research avenues to test these hypotheses.

Direct Impacts of Climate Change. Changes in annual rainfall and El Niño–Southern Oscillation have been implicated as important drivers of population demography among Neotropical birds. Both excessive rainfall in La Niña years (25, 39, 40) and too little rainfall in El Niño years (38, 41–43) can have negative demographic consequences on tropical bird populations, including reduced survival (41, 42), population growth rates (38), and recruitment (38, 43). For example, nearly one-third of 20 common bird species captured at our study site exhibited reduced annual population growth rates in response to longer dry seasons (38). Although mean annual precipitation, mean dry-season length, and the Southern Oscillation Index (SOI; as indicated by historical trends obtained from Barro Colorado Island, a research station 8 km from our study site) appear to have remained relatively unchanged over the 44-y study period (*SI Appendix, Fig. S10*; climatic data derived from https://biogeodb.stri.si.edu/physical_monitoring), we acknowledge that the lack of long-term change in mean rainfall metrics and SOI does not provide definitive evidence that rainfall is not playing a role in the

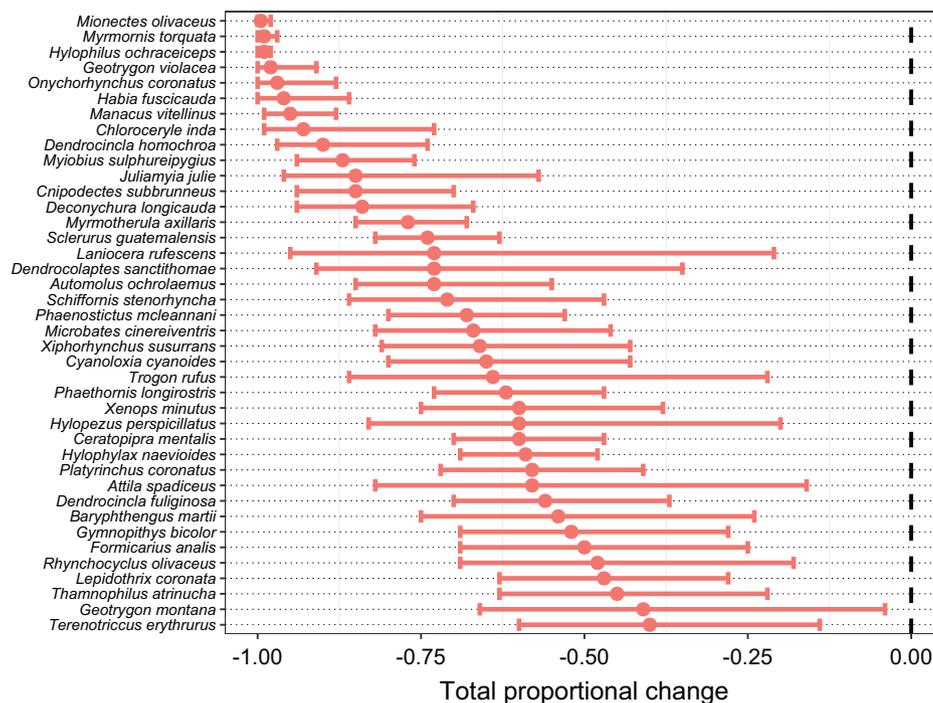


Fig. 2. Total proportional losses in abundance of the 40 species whose populations declined across the 44-y sampling period (1977 to 2020) at the Limbo plot, Parque Nacional Soberanía, Panama. For each species, the mean estimate of total proportional change and 95% BCIs are shown.

observed declines. For example, work in Costa Rica found that the amount of rainfall over short time periods (i.e., 72 h) altered birds' ability to forage, with subsequent impacts on survival and migration propensity (44). Therefore, there is merit in further study of the interannual associations between abundances and rainfall-related climatic variables and, in particular, the role of extreme drought and/or rainfall.

In addition to rainfall regime, warming temperatures have been linked to bird declines worldwide (45, 46), although evidence in tropical areas remains limited. For example, a 15-y population study of rufous-and-white wrens (*Thryophilus rufalbus*) in northwestern Costa Rica found that survival was lower in hotter years (47). Warming-associated range shifts of lowland tropical bird species have resulted in decreased abundances and local extirpation of higher-elevation species from several localities (7, 8, 10). Whereas we found no evidence of long-term changes in maximum temperature at our study site, mean temperature has increased by $\sim 1^\circ\text{C}$, and minimum temperature has increased by $\sim 0.5^\circ\text{C}$ across the study period (*SI Appendix, Fig. S10*). Future studies that delve into the possible mechanistic links between temperature regime and population trends (i.e., assessing associations between annual abundances and temperature metrics, as described above) will be necessary to test the influence of temperature on bird declines.

Indirect Impacts of Climate Change. The population declines we observed could be driven by indirect impacts of climate change on birds' food resources (bottom-up impacts) or predators/parasites (top-down impacts). With respect to bottom-up processes, changes in climate could be having cascading impacts on bird populations via direct effects on arthropod prey (i.e., for insectivores), fruit production (i.e., for frugivores), or flower availability (i.e., for nectarivores). For example, tropical insects exhibit disproportionately narrow thermal tolerances and sensitivity to climate change relative to temperate counterparts (48, 49). Therefore, warming- or desiccation-induced declines of tropical invertebrates (e.g., ref. 50) could be indirectly driving

bird declines via reduced food availability (e.g., refs. 51 and 52). At our study site, for example, some insectivorous bird species exhibited reduced juvenile recruitment and population growth rates in response to seasonal drought (38), which could be mediated by reduced arthropod abundance. Increased mean annual temperature, maximum annual temperature, temperature anomalies, and precipitation anomalies have all been shown to cause declines in tropical arthropod richness (e.g., refs. 50 and 52), and short-term changes in temperature and rainfall have been linked to shifts in insect activity (reviewed in ref. 53).

In a similar vein, changes in rainfall, temperature, and dry-season length can strongly impact fruit and nectar availability, with possible indirect effects on frugivore and nectarivore populations. For example, increased precipitation anomalies can result in widespread failure in fruit production (54) and shifts in fruiting phenology (55); and longer dry seasons can decrease fruit, flower, and seed production (56). In particular, El Niño events, which affect seasonal rainfall and dry-season length, have been documented to have both negative (e.g., refs. 38 and 56) and positive (e.g., refs. 39 and 40) effects on tropical frugivores and nectarivores. Recent evidence suggests that adults of tropical forest bird species are able to survive El Niño events or seasonal drought (e.g., refs. 42 and 57) but may modulate or forego breeding entirely in favor of self-maintenance during periods of low rainfall and/or low food availability (43, 58, 59), thereby driving reduced population growth rates. Future studies that directly measure food resources in relation to climate and bird abundance (e.g., ref. 58) and that focus on juvenile recruitment are needed to tease apart the potential bottom-up impacts of climate warming on resource availability and bird populations.

Climate change could also be exerting top-down effects of predators or parasites on bird demography. Higher temperatures and increasing precipitation have been associated with increased prevalence of blood parasites across an elevation gradient in Australian birds (60), although very few long-term studies have documented changes in avian blood parasite

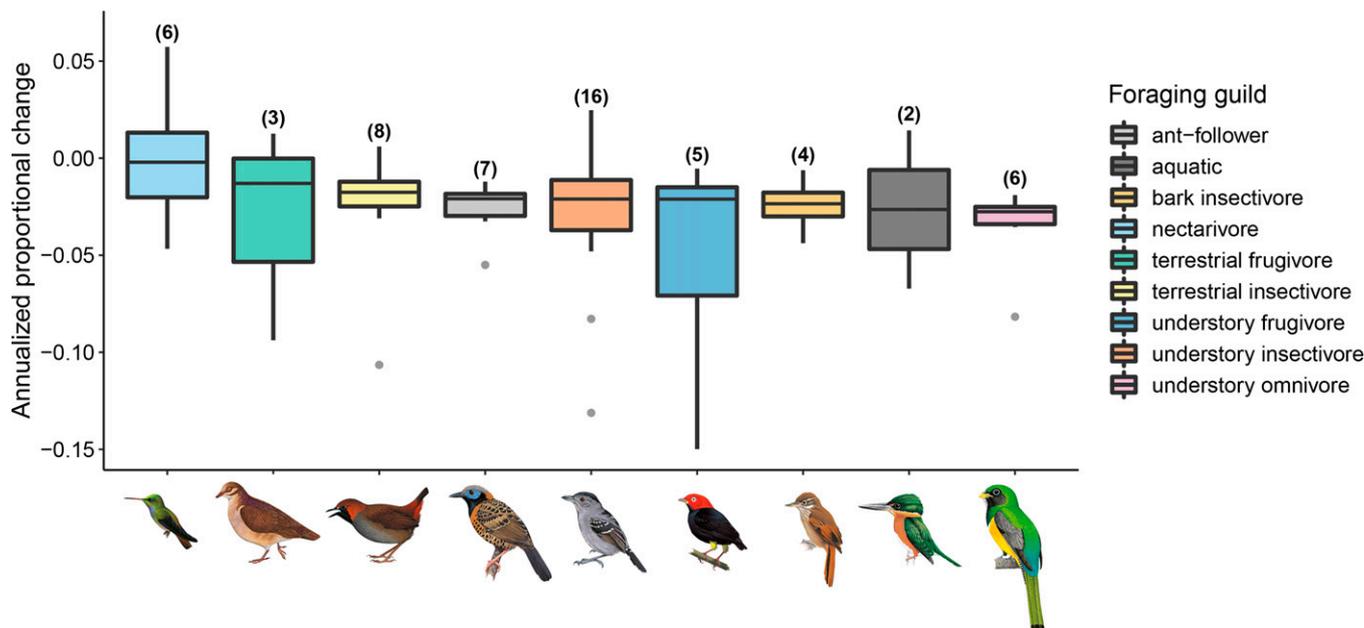


Fig. 3. Box plots of annualized proportional change in abundance by foraging guild for the 57 focal species included in the study. Exemplar species and sample sizes by guild, in order from left to right: nectarivore (crowned woodnymph [*Thalurania colombica*]; $n = 6$); terrestrial frugivore (ruddy quail-dove [*Geotrygon montana*]; $n = 3$); terrestrial insectivore (black-faced antthrush [*Formicarius analis*]; $n = 8$); ant-follower (ocellated antbird [*Phaenostictus mcleani*]; $n = 7$); understory insectivore (black-crowned antshrike [*Thamnophilus atrinucha*]; $n = 16$); understory frugivore (red-capped manakin [*Ceratopira mentalis*]; $n = 5$); bark insectivore (plain xenops [*Xenops minutus*]; $n = 4$); aquatic (American pygmy kingfisher [*Chloroceryle aenea*]; $n = 2$); and understory omnivore (black-throated trogon [*Trogon rufus*]; $n = 6$). Horizontal dashed line indicates no change in abundance.

prevalence due to climate change (reviewed in ref. 61). An 11-year study of lance-tailed manakins (*Chiroxiphia lanceolata*) in Panama found that nestlings had increased lesions, reduced growth rates, and lower fledging success in drier El Niño years (41), suggesting possible top-down control by parasites, but more investigation is needed to determine the generality of these results. Similarly, predation pressure is predicted to increase globally with rising temperatures (62), and rainfall-induced shifts in predator-prey dynamics have been documented in other systems (63–65). However, we are unaware of any studies documenting the impacts of climate on predator-prey dynamics among tropical birds, and the role of climate-induced top-down impacts remains largely untested.

Local and Regional Habitat Changes. Despite the absence of major land-use change within the reserve, local structural changes in the forest at our study site and regional changes in forest connectivity likely underlie the declines of certain species. In particular, species associated with edge habitats and higher-elevation or wetter forests were all present at low initial abundances at the beginning of the study and likely have declined or been extirpated due to loss of preferred local habitats or regional connectivity (*SI Appendix, Table S3*). For example, three edge species (golden-collared manakin [*Manacus vitellinus*], red-throated ant-tanager [*Habia fuscicauda*], and royal flycatcher [*Onychorhynchus coronatus*]) exhibited some of the steepest declines and greatest proportional losses as local successional changes have led to forest maturation along Pipeline Road, consistent with declines and extirpations of edge species in response to forest maturation at nearby Barro Colorado Island, Panama (66). In addition to these changes in local habitat structure, loss of regional connectivity between our lowland site and higher-elevation forests east of the Isthmus of Panama and wetter forests on the Caribbean side of the Isthmus (*SI Appendix, Fig. S2*) may be partially responsible for a few select species' declines (i.e., see *SI Appendix, Table S3*). For example,

the olive-striped flycatcher (*Mionectes olivaceus*), typically a higher-elevation species known to make seasonal elevational movements (e.g., ref. 67), lost >98% of its initial abundance at our study site. Similarly, the two species whose western geographic range limits in Panama occur in the Canal Zone (i.e., violaceous quail-dove [*Geotrygon violacea*] and wing-banded antbird [*Myrmornis torquata*]), where our study site is located, have likely become locally extirpated. Thus, loss of connectivity may be contributing to population decreases of these species via inhibition of seasonal movements (e.g., ref. 68) and Allee effects on small range-edge populations. Our results corroborate studies of bird communities in Costa Rica (28), Colombia (29), and Ecuador (30) showing that even the loss of regional forest connectivity outside of large reserves can have negative impacts on biodiversity within the reserve.

Conclusions. Our findings of systematic avian population declines in intact tropical forests bolster the available evidence demonstrating declines in bird abundance across diverse biomes and disparate taxa worldwide (15–19). The widespread declines of tropical birds in a large, protected area are a particular cause for concern. Unfortunately, it is difficult to contextualize these results among tropical birds due to the relative dearth of long-term avian population studies from the tropics (69). Despite containing disproportionately high levels of biodiversity, tropical regions continue to be understudied due to a lack of funding and resources (1). Indeed, the vast majority of bird population studies in the Neotropics have focused on the impacts of land-use change and forest fragmentation on population trends precisely because habitat loss and deforestation are such pressing issues in the tropics (4, 70). Our study bolsters the sparse available evidence (e.g., refs. 25 and 26) suggesting that the current bird communities in relatively undisturbed tropical forests may actually represent profound shifts from historical baselines. The next logical step toward understanding and possibly preventing further declines is identifying the

underlying ecological mechanisms. To accomplish this, intensive, long-term studies of individual species will likely be needed to drill down to the factors causing the declines.

Materials and Methods

Study Site. We conducted our research in Parque Nacional Soberanía, a ~22,000-ha protected reserve located in the Republic of Panama (9° 9' 35" N, 79° 44' 36" W). Our study site was a relatively flat, ~600-ha circular basin of lowland tropical moist forest surrounded by steep ravines and dissected by numerous streams (71). One mist net line (Hunt Club) was established in 1968 to 1969 (72, 73), with several additional lines, including Ridge, established in the mid-1970s (74). Hunt Club and Ridge lines, the focus of this analysis, are ~800 m apart within a larger 104-ha study area called the Limbo plot (SI Appendix, Fig. S1), established around these net lines in the mid-1990s (see ref. 71 for details). The Limbo plot is characterized by a distinct dry season (January to April) and rainy season (May to December), with 90% of annual precipitation (\bar{x} = 2600 mm) occurring during the rainy season (71, 72). Elevation across the plot ranges from 35 to 225 m, and forest age varies across the plot, consisting mostly of old secondary forest (i.e., >100 y old) with some remnant patches of mature, old-growth forest.

Although the Limbo plot is located within a protected reserve that has not undergone significant forest fragmentation or land-use change since the inception of the net lines, habitat changes have occurred both locally (i.e., adjacent to the net lines) and regionally (i.e., within the Republic of Panama) during the course of the study. On a local scale, the plot is bisected by Pipeline Road, which was originally composed of paved blacktop and was maintained as a broad, open corridor from its initial construction in the 1940s until the late 1970s. The road used to have a 25-m buffer of second-growth habitat on either side of the road that was large enough to support populations of edge species that were present at the beginning of the study (71, 72). The buffer strip was abandoned to natural succession after the establishment of Parque Nacional Soberanía in 1980, however, and Pipeline Road has turned into a 5-m-wide dirt road surrounded primarily by closed-canopy forest (71). Additionally, large treefalls have been recorded regularly at and around the net lines, resulting in short-term changes (e.g., annual or decadal) in species presence, absence, and abundance (74–76). On a regional scale, deforestation and human development have reduced connectivity of Parque Nacional Soberanía to higher-elevation forests to the east (e.g., Cerro Jefe, Cerro Azul) and wetter Atlantic coastal forests to the north (e.g., Parque Nacional San Lorenzo, Rio Piedras, and Portobelo areas; see SI Appendix, Fig. S2 for a detailed history of land-use change in the Canal Area).

Sampling Bird Populations. Twice each year from 1977 to 2020—once in the dry season (March) and once in the rainy season (July)—we set up mist nets (12 × 2.6 m, 36-mm mesh) at each net line and captured birds. Exceptions included no sampling in 1991, sampling only once per year in 3 y (1992, 2018, and 2020), and occasional slight shifts of sampling dates in the dry season (April 2002 and 2018) or rainy season (June 1977, 2002, and 2017; August 2004). Prior to 1995, the number of nets used during each sampling period varied at both the Ridge (range: 12 to 18; median: 15) and Hunt Club (range: 11 to 18; median: 15) sites, and sampling was concluded when 100 total captures were recorded. Starting in 1995, constant-effort sampling was adopted, with 20 to 21 nets and ~600 total net hours of sampling time accumulated (i.e., 06:00 to 18:00 on days 1 to 2, 06:00 to 12:00 on day 3) per site for each sampling interval. We accounted for this variation in sampling effort (SI Appendix, Fig. S3) and provide details in *Statistical Analyses*. Nets were temporarily closed and sampling was paused during heavy rains or other inclement weather and resumed when conditions improved. We marked all individuals with uniquely numbered aluminum bands and identified them to the species level using expert knowledge and field guides (67, 77). We excluded species that were infrequently captured, such as canopy species and large-bodied species (e.g., toucans, raptors), from the subsequent statistical analyses. We also excluded migratory species (n = 16), as we were primarily interested in the trends of resident tropical species, and only four migratory species had n ≥ 20 captures.

Statistical Analyses. For each species, we used the number of unique individuals captured during each sampling period as an index of local abundance (e.g.,

ref. 25). This index is expected to be reliable if individuals do not develop behavioral avoidance of mist nets due to frequent sampling of the same locations (78). We minimized this risk by sampling at each site for only 3 to 5 d twice per year (5 to 7 mo between sampling periods), thereby reducing the likelihood of net avoidance (see refs. 74 and 79). We tested for evidence of net avoidance by using capture-mark-recapture models to examine temporal variation in recapture probabilities across the study for eight common species (SI Appendix, Fig. S4). Whereas we did observe declines in capture rates within a single sampling period (i.e., during the 3- to 5-d period at a given net line in a given season), we did not detect systematic declines between subsequent sampling periods, which would be expected if net avoidance were occurring. Moreover, recapture probabilities varied substantially among years but did not systematically increase or decrease during the study (SI Appendix, Fig. S4), indicating that the number of unique individuals captured was a reliable index of abundance.

Although abundances can vary idiosyncratically over shorter timescales, our main objective was to estimate long-term trends (if any) across the entire 44-y time series. We registered a total of 14,964 captures, comprising 149 species and 33 families (SI Appendix, Table S1), over the course of 84,548 net h between 1977 and 2020. Models for infrequently captured species produced uninformative credible intervals, so we excluded species with n < 20 captures (n = 87 species; SI Appendix, Table S1) from the analysis, resulting in a total of 14,210 unique individuals of 57 resident bird species (SI Appendix, Table S2). Preliminary analyses revealed a strong effect of season (i.e., differences between dry and rainy seasons) and net line (i.e., differences between Hunt Club and Ridge) on the number of captures for some species, so we included both as covariates in our analyses to account for their potential impacts on variation in abundance.

For all 57 species, we used the following workflow to identify and estimate an appropriate trend model for each species in a generalized linear modeling framework. First, we fit an additive Poisson model with year, season, and site as model terms; the number of unique individuals captured as the response variable; and the number of net hours as an offset term to correct for the temporal variation in sampling effort across the years (SI Appendix, Fig. S3).

The number of unique individuals captured in a given sampling period can be considered to be a realization of a random variable Y_{ijk} , where

$$E[Y_{ijk}] = \mu_{ijk}, \text{ with } Y_{ijk} \sim \text{Poisson}(\mu_{ijk})$$

$$\log(\mu_{ijk}) = \beta_0 + \beta_1 \cdot \text{year}_i + \beta_2 \cdot \text{season}_j + \beta_3 \cdot \text{site}_k + \text{offset}(\log(\text{nethours}_i))$$

in which i is the sampling year index, j is the season index, k is the site index, μ_{ijk} is the mean, and $\beta_0 \dots \beta_3$ are the coefficients.

We then assessed the standard Poisson model for evidence of overdispersion by comparing with simulated data using the *dispersion_check* function of the R package *inltools*. We also assessed whether there was potential for zero inflation (i.e., proportion of zeros in the response variable was >50%; ref. 80), in which case we also fit a zero-inflated Poisson model; specifically, the model adds a point mass at zero to the standard Poisson model using a mixture model framework (i.e., a multiplicative approach). In this case, the number of unique individuals captured in a given sampling period follows a more complex distribution:

$$P(Y_{ijk} = y_{ijk} | \beta_0, \beta_1, \beta_2, \beta_3, \pi_{ijk}) \sim \begin{cases} \pi_{ijk} + (1 - \pi_{ijk}) \cdot e^{-\mu_{ijk}} & y_{ijk} = 0 \\ (1 - \pi_{ijk}) \cdot f_{\text{Poisson}}(y_{ijk} | \beta_0, \beta_1, \beta_2, \beta_3) & y_{ijk} > 0 \end{cases}$$

where π_{ijk} is the probability that $y_{ijk} = 0$ (i.e., the probability that there will be a zero count for that species at a given site in a given season and year), and the Poisson model component is identical to that above.

For species (n = 9) in which there was evidence of model overdispersion, after accounting for zero inflation (as assessed using the *dispersion_check* function), we fit negative binomial models:

$$E[Y_{ijk}] = \mu_{ijk}, \text{ with } Y_{ijk} \sim \text{Negative Binomial}(\mu_{ijk}, \theta)$$

$$\log(\mu_{ijk}) = \beta_0 + \beta_1 \cdot \text{year}_i + \beta_2 \cdot \text{season}_j + \beta_3 \cdot \text{site}_k + \text{offset}(\log(\text{nethours}_i))$$

where θ is the variance, and all other terms are analogous to those in previous models.

We used the Watanabe-Akaike information criterion to confirm the best-supported model for each species. In all cases, we confirmed that there was no

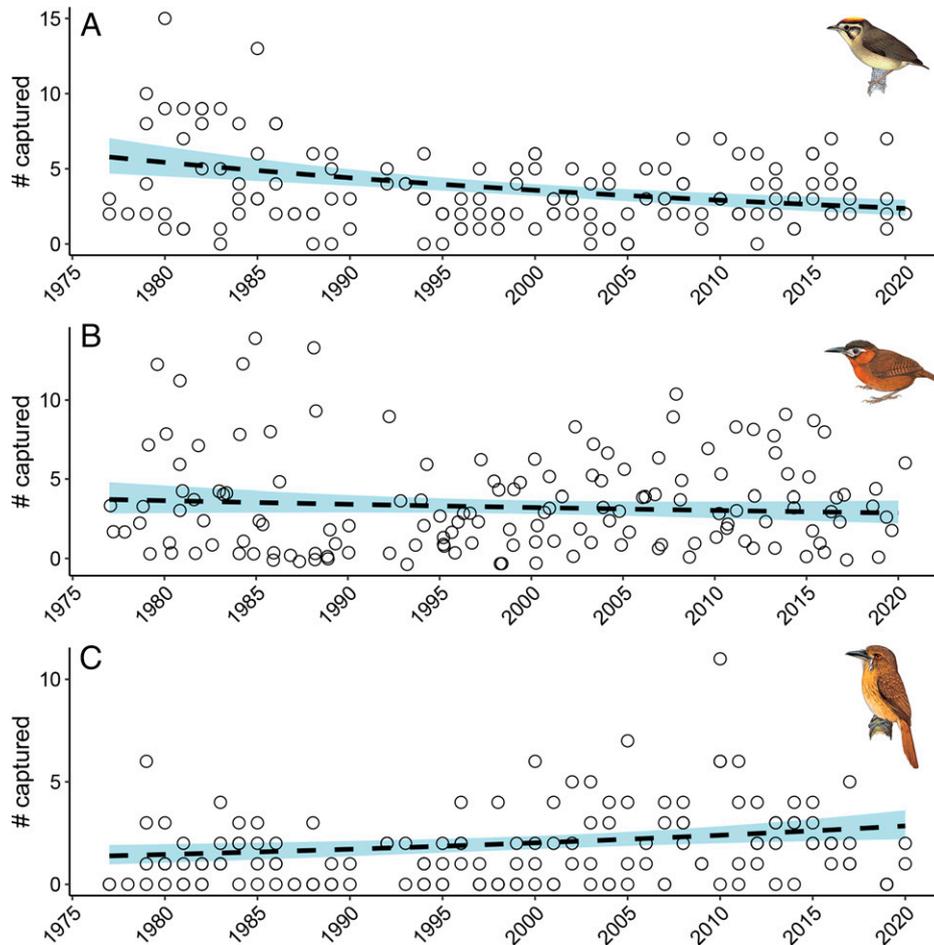


Fig. 4. Number of captures and predicted values from species-specific models for three representative focal species captured across the 44-y sampling period (1977 to 2020) at the Limbo plot, Parque Nacional Soberanía, Panama. Exemplar bird species include (A) golden-crowned spadebill (*Platyrinchus coronatus*; decreased in abundance), (B) song wren (*Cyphorhinus phaeocephalus*; no apparent change in abundance), and (C) white-whiskered puffbird (*Malacoptila panamensis*; increased in abundance). See *SI Appendix Fig. S6* for graphical model predictions for all 57 focal species.

evidence of temporal autocorrelation in the residuals for the best-supported model, such that autoregressive models were not required. The fitted model was used to simulate data to compare with the raw data to ensure that the model fitted the data well (i.e., to conduct a posterior predictive check; ref. 81), using the *distribution_check* function of *inlatools*.

Model residuals were also examined to confirm that overall linear trends were well supported for all species (i.e., that there was neither systematic nonlinearity nor influential observations, following ref. 82), with the acknowledgment that this does not capture the smaller-scale fluctuations inherent in the 44-y sample. Models were estimated using integrated nested Laplace approximations (INLA; ref. 83) with the R package R-INLA (<https://www.r-inla.org>).

For each species, we extracted the slope associated with year (i.e., β , the rate of change in the predicted number of unique individuals captured per year; see *SI Appendix, Fig. S2* for raw β estimates). Because the loss of a specific number of individuals has differing consequences depending on the initial population size (e.g., the loss of 5 individuals from a population of 20 has greater consequences than, for example, the loss of 5 individuals from a population of 100), we chose to use metrics of proportional loss (i.e., percent decline) to facilitate comparison of population trends across species. Specifically, we derived two interrelated but distinct aspects of the trend from the slope parameter β : 1) the annualized proportional change in abundance, $e^{\beta} - 1$ (i.e., the multiplicative change in the population over a single year for every unit change in the covariate); and 2) the total proportional change in abundance, $e^{\beta t} - 1$, where $t = 44$ (i.e., the multiplicative change in the population integrated over the entire 44-y study period). The annualized proportional change is synonymous with how rapidly or steeply a population changed in abundance, whereas the total proportional change estimates how much a population changed in abundance since the study began. In both cases, credible intervals and point estimates were

transformed based on the marginal distributions of the slope parameter, which we used to characterize the magnitude and uncertainty of estimated population trends over time. We designated trends as “increasing” if the annualized proportional change was positive and its 95% Bayesian Credible Intervals (BCIs) did not overlap zero, “no change” if its BCIs overlapped zero, and “decreasing” if the annualized proportional change was negative and its BCIs did not overlap zero (see Fig. 4 for examples). As an additional metric of total population change, we calculated the difference in each model’s posterior mean predicted values between the first (i.e., predicted number of individuals in 1977) and last years (i.e., predicted number of individuals in 2020) of the study (hereafter, “ Δn ”). Δn can be considered an estimate of how many individuals would be expected to be gained or lost from the total number of captures on the two net lines (standardized for constant effort) over the course of the study (i.e., a more negative Δn indicates that fewer individuals would be expected to be captured at the end of the study period).

We next examined the possible effect of three ecological traits (body mass, foraging guild, local abundance) on temporal trends in species’ abundances. For each species, we took the average body mass from all individuals of the given species from the 44-y mark-recapture dataset. We categorized species into nine foraging guilds based on the designations proposed in reference (84) and previously used at our study site (72, 85) and in other studies (e.g., ref. 25): “army-ant-follower,” “aquatic,” “bark insectivore,” “nectarivore,” “terrestrial frugivore,” “terrestrial insectivore,” “understorey frugivore,” “understorey insectivore,” and “understorey omnivore.” We expected that species captured less frequently (i.e., with lower population densities) at the beginning of the study might be more likely to decline over time. Therefore, to establish a baseline metric of local abundance, we ranked all 57 species from most (ranked 1) to least (ranked 57) abundant by tabulating the total number of unique captures across the first 5 y of the study (1977 to 1981).

To assess the influence of ecological traits on estimated trends among the focal species, we tested for associations among the three ecological covariates and the annualized proportional change in abundance. We constructed a generalized linear mixed model with a Gaussian error distribution in the R package "MCMCglmm" (86). To account for variation in uncertainty around the estimates for each species, we weighted species' trend estimates by the reciprocals of their estimated variances. We tested for and found no interactions or evidence of collinearity among the three covariates, nor was there evidence of nonlinear relationships with trends for any of the covariates, so we proceeded with a global additive model including all three covariates as fixed effects. To control for phylogenetic relationships among the focal species, we downloaded 1,000 randomly selected phylogenetic trees from birdtree.org (87) that used the phylogeny of ref. 88 as a backbone. We generated a consensus tree from these 1,000 trees using the consensus function in the R package "ape" (89). We then included the inverse of the correlation matrix of the consensus tree as a random phylogenetic effect in the model (following ref. 90). To assess phylogenetic signal, we estimated Pagel's λ (91) in the residual error of the model and used these estimates to scale the model. λ can range from 0 to 1, with a value of 0 indicating no phylogenetic signal and a value of 1 indicating Brownian motion. The intercept-only model included flat priors and was run for 100,000 iterations with a burn-in of 10,000. We report the posterior mean effects, the 95% credible interval (CI; lower and upper CI), and Markov chain Monte Carlo P value (the probability that the posterior distribution crosses zero) of the model.

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Data Availability. All study data are included in the article and/or supporting information and are also available in GitHub at <https://github.com/henryPollock/Panama-bird-declines>.

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